PHYLOGENY AND ZOOGEOGRAPHY OF THE GHARIAL, *GAVIALIS GANGETICUS* (GMELIN) (REPTILIA, CROCODILIA)[1]

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(With a text-figure)

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The accepted theory is that the family Hylaeochampsidae of the order Eusuchia branched into the family Gavialidae on one side and into the families Stomatosuchidae, Nettosuchidae and Crocodylidae, on the other. The zoogeography of *Gavialis,* based on systematics, continental drift, anatomy and physiology, suggests that *Gavialis* has affinities with both *Tomistoma* and *Mesosuchia.* Like *Tomistoma,* it is an inhabitant of fresh water and both probably had ancestors adapted to salt water. The buccal morphology of *Gavialis* resembles species of marine origin.

The *Gavialis* drifted from India to other Asian countries during the Miocene and then it remained confined to India in the pleistocene respectively. Fossil records also refer to its presence in Africa and South America. The current existing populations of *G. gangeticus* is restricted to the Indian subcontinent.

INTRODUCTION

Many theories of evolution, phylogeny and zoogeography of crocodilians have been propounded. The 'phylogeny and ancestral relationship of the crocodilian genus, *Gavialis* is still debatable (see Mook 1934, Lull 1944, Sill 1968, Densmore 1983) although the phylogeny of the Crocodilia in reference to taxonomy has been dealt in detail by Sill (1968).

Densmore and Dessauer (1982) and Densmore (1983) employed biomedical and immunological techniques while Pandey (1991) explained the role of endocrinology in the phyletic picture of reptiles. Subsequently, Blofield *et al.* (1992) used haematological implications to understand the phylogenetic relationship.

Sill (1968) reviewed the zoogeography and continental dispersal of eusuchian crocodilians. However, little information is available on the phylogeny, zoogeography, and dispersal of *Gavialis* (Hecht and Malone 1972, Buffetaut 1978, 1982; Buffetaut and Thomas 1981). Taplin and Grigg (1989) explained that eusuchian zoogeography is based on new information pertaining to their systematic relationship and physiological capacity for marine dispersal and on fossil records. The available data is reviewed here.

A. PHYLOGENY

The phylogeny of eusuchian crocodilians is based on the fossil history and biology of the existing crocodilian species.

Taplin and Grigg (1989) discussed the phylogeny of *Gavialis* and concluded that

* Anatomical and physiological adaptations to marine existence have played an important role in eusuchian history.

* *Gavialis* and *Tomistoma*, now restricted to freshwater, may have been derived from ancenstors adapted to salt water.

— The buccal morphology of *Gavialis* suggests that it also has a marine ancestry.

— The systematic affinities of *Gavialis* are uncertain, lying perhaps with *Tomistoma* and on other interpretations with Mesosuchia.

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Densmore (1983) and Densmore and Owen (1989) discussed the eusuchian zoogeography on the basis of biomedical and immunological studies of existing crocodilian species, highlighting:

(i) The living eusuchians form a monophyletic group with three major lineages: crocodiles, alligators and gavialids.

(ii) *Gavialis* and *Tomistoma* are members of a monophyletic group, more closely related to the crocodile lineage than to the alligators.

(iii) *Gavialis* and *Tomistoma* are members of a common lineage. Buffetaut and Thomas (1981) and Buffetaut *et al.* (1984) proposed that *Gavialis* is derived from tomistomines which originated in the old world (probably Africa) in the early Tertiary and migrated to South America and India.

The physiological capabilities of the lingual glands in crocodilians have been taken into account to postulate the evolution and zoogeography in Eusuchia,

Taplin *et al.* (1985) and Taplin and Grigg (1989) noted that lingual gland pores are evident on the tongues of both *Tomistoma* and *Gavialis* and that the glands in *Gavialis* are minute in size and have a very low secretory capacity comparable to the alligatorids than examined. They also recorded that the general appearance of the tongue and buccal cavity of both *Gavialis* and *Tomistoma* is distinctively crocodyline rather than alligatorid. The explanation of the similarities in buccal structure is seen in *Tomistoma* and *Gavialis*, the salt glands and their associated buccal modifications have developed during adaptation to a marine existence. They considered the possibilities of adopting Buffetaut's view that gavialids are derived from tomistomines or considering Tarsitano's (1985) view that gavialids originated independently from a thalatosuchian stock and concluded that buccal anatomy of *Gavialis* and *Tomistoma* are crocodyline and both have a common lineage, and buccal morphology of *Gavialis* shows its ancestery from marine stock. However, it is still controversial as to whether the gavialids are derived from tomistomines or Mesosuchia, or originated independently from Thalatosuchians (Fig. 1).

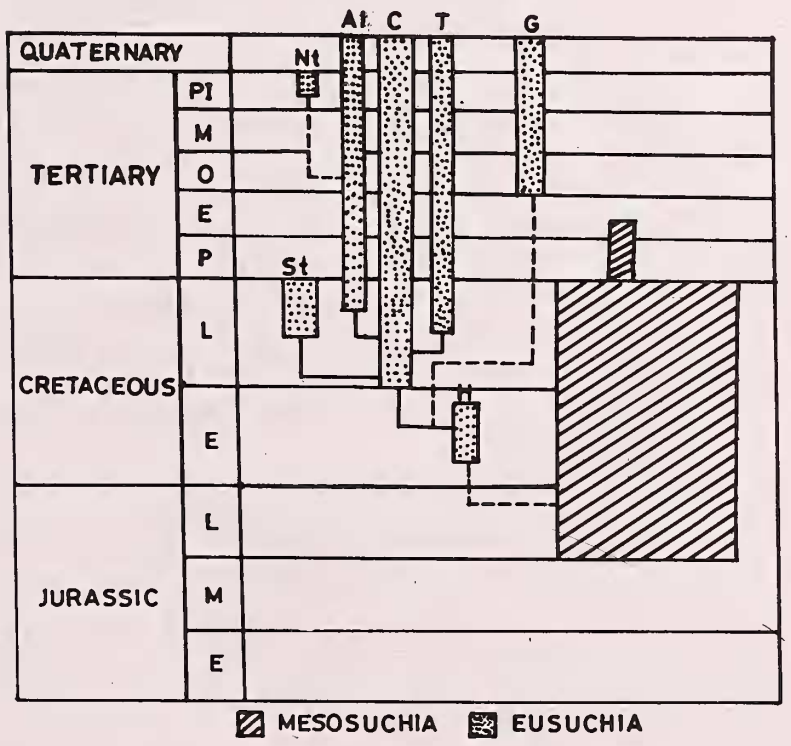

Fig. 1. Phylogeny of family Gavilidae. Al-Alligatorinae; C-Crocodilinae; G-Gavialidae; H-Hylaeochampsidae; Nt-Nettosuchidae; St-Stomatosuchidae; T-Tomistominae.

B. Classification of *Gavialis gangeticus*:

The family Gavialidae belongs to the suborder Eusuchia of the Order Crocodilia. The animals of the Order Crocodilia came into existence during the middle Triassic period. The order includes five suborders, Sill (1968)

1. Suborder : Archeosuchia Sill, 1967. Extinct
2. Suborder : Protosuchia Mook, 1934. Extinct
3. Suborder : Mesosuchia Huxley, 1875. Extinct
4. Suborder : Sebecosuchia Simpson, 1937. Extinct
5. Suborder : Eusuchia Huxley, 1875. Living.

The only living Suborder Eusuchia of the Order Crocodilia has five families: 1. Hylaeochampsidae; 2. Stomatosuchidae; 3. Gaviallidae; 4. Nettosuchidae; 5. Crocodilidae.

The family Hylaeochampsidae is the most primitive and has given rise on one side to the families Stomatosuchidae, Nettosuchidae and Crocodylidae and on the other to the family Gavialidae (Fig. 1).

The family Gavialidae is represented by one surviving genus *Gavialis* containing a single species *Gavialis gangeticus* Gmelin (1789), commonly know as the gharial.

The distinguishing characters of *Gavialis* listed below suggest its relatively long isolation from other crocodilies.

i. Depression of postorbital bar; ii. Jaw articulation of different angle and shape; iii. Elongation of snout by extension of only the maxillaries instead of both maxillaries and nasals, as in other longirostrine crocodiles.

The long slender snout is an adapation to a diet consisting almost exclusively of fish. *Gavialis* possesses an elongated snout, characteristic skull profile and close spacing of teeth. The genus *Gavialis* has been confined to the Indian peninsula from the early Miocene to the present time (Lull 1944).

C. Zoogeography:

The Zoogeography of *Gavialis* was initially based on the fossil history and evolution of the eusuchians. This has been continuously modified taking into account the biology of the species. The debate has now centered on the anatomy and physiology of *Gavialis* relative to its zoogeography and dispersal.

Buffetaut (1978, 1982, 1985 a, b) proposed that the appearance of gavialids in the Oligocene of South America called for a trans-Atlantic migration across the developing South Atlantic Ocean in the upper Eocene or early Oligocene. Buffetaut and Thomas (1981) and Buffetaut *et al.* (1984) proposed that *Gavialis* is essentially a highly derived tomistomine which originated in the Old World (probably Africa) in the early Tertiary and migrated to South America and India. Buffetaut interpretations are rejected by Tarsitano *et al.* (1989) whose analysis of cranial morphology and hind limb, and cranial musculature points to a separate origin of the gavialids, perhaps from the Mesozoic thalattosuchians. Taplin and Grigg (1989) discussed a detailed scenario for the zoogeography of eusuchians using a physiological perspective and the interpretations of many workers and concluded that the early Tertiary disjunction of gavialid distribution was between Africa and South America. They further discussed a tomistomines and gavialid lineage. The salient features dealing with the zoogeography of gavialids are:

(1) Longirostrine crocodilians regarded as being from the tomistomine lineage, are from the upper cretaceous and early tertiary of Europe and North America.

(2) The proposition that gavialids belong to the tomistomines lineage, as it is presently known, requires either an Oligocene crossing of the South Atlantic (a barrier some 1000 km wide), or convergent evolution of similar skull form in New and Old World lines which separated at a much earlier date (Buffetaut 1980, 1985 a, b, c). Taplin and Grigg (1989) added that gavialids are derived tomistomines as they are presently recognized and include marine and littoral forms.

(3) The gavialids are considered by Buffetaut (1985 b) to have had at least three branches, the Indian and Asian *Gavialis* species, a South American branch and the widespread *Gavialosuchus* of North American lines (known only from fossils of fresh water deposit). The occurrence of *Gavialis* in the Pleistocene of Java is inconsistent with dispersal of a derived freshwater stock through the Asian archipelago. *Gavialosuchus* enjoys a much more widespread distribution than other gavialids and is characteristic of the littoral and marine strata of the Atlantic seaboard of Europe, Africa and North America.

(4) The fossil record is inconsistent with the view that the sole surviving modern freshwater gavialid and *Tomistoma* are derived from marine adapted ancestors and retain some characteristic physiological and anatomical specializations.

(5) Gavialids might have close affinities with the characteristically marine thalattosuchians than are Mesosuchia, and are considered to be a

secondarily derived fresh water crocodilian.

On the basis of the above discussions and fossil history one view is that the gavialids are tomistomines that originated in the Old World (Africa) and migrated to South America and India. A second view holds that gavialids had three branches: (i) The Indian and Asian gavialids, (ii) The South American branch and (iii) The *Gavialosuchus* of North America. This subject deserves more study for a final conclusion.

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